EFFECTS OF CATTLE GRAZING, INSECT INTERACTIONS AND POPULATION ECOLOGY OF SNAKE RIVER GOLDENWEED (*HAPLOPAPPUS RADIATUS*)

Final Report

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PREFACE

This report is the result of a cooperative Challenge Cost Share project between the Institute for Applied Ecology (IAE) and a federal agency. IAE is a non-profit organization dedicated to natural resource conservation, research, and education. Our aim is to provide a service to public and private agencies, individuals, and the environment by developing and communicating information on ecosystems, species, and effective management strategies and by conducting research, monitoring, and experiments. IAE offers educational opportunities through 3-4 month internships. Our current activities are concentrated on rare and endangered plants, invasive species, and habitat restoration.

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EXECUTIVE SUMMARY

1. Background

Snake River goldenweed (*Haplopappus radiatus*) is a rare plant of eastern Oregon and adjacent western Idaho. The species is listed as endangered by the State of Oregon Department of Agriculture and the Oregon Natural Heritage Program. It is considered a Sensitive Species by the Bureau of Land Management. The species occurs in arid shrub-steppe rangeland and many populations are on federally managed lands that are subject to livestock grazing. This report is the result of a long-term study intended to document the effects of livestock grazing on Snake River goldenweed and identify other factors affecting populations of the species.

2. The Study

This study was initiated in 1991 in Baker County, Oregon on lands managed by the Vale District, BLM. Five pairs of study plots were established, one plot fenced to exclude cattle and the other left unfenced. In each year from 1991 through 2001, plants within the study plots were mapped and measured. Plant size and reproduction was compared for grazed and protected plots each year of the study, factors such as seasonal precipitation were examined as factors affecting the species biology, and a population viability analysis utilizing on demographic models was conducted.

3. Effects of Grazing

Plants exposed to grazing were smaller, flowered less, and had lower population growth rate than protected plants by the end of the study. However, there was a substantial time-lag (six to eight years) between when fences were constructed and when this effect was detected. There were also negative correlations between the frequency of grazing on Snake River goldenweed and plant flowering and population growth. Despite these effects, there was no detected difference in population viability as measured by extinction probability in grazed vs. fenced plots. More sophisticated models that take into account seasonal precipitation and intensity of grazing in any given year may yield different results.

4. Effects of Seasonal Precipitation

Seasonal precipitation had significant positive effects on Snake River golden weed flowering, seed production, and population growth, but negative effects on seed predation and grasshopper damage.

5. Seed Predators and Grasshoppers

Seed predation by insect larvae (weevils, moths and midges) was intense in some years, killing at least half of the seeds in four of the ten years sampled. Grasshoppers also had substantial impacts, consuming over 60% of plant foliage in 2 of eleven years sampled and lowering seed set. These levels of seed damage and herbivory may have long-term impacts on this species.

6. Recommendations

Livestock grazing in populations of Snake River goldenweed should be minimized to allow plants to achieve large size and reproduce well. It is likely that other populations of this species that occur in similar habitats subject to grazing have smaller plants that reproduce less and have lower population growth rates, on average, than populations in non-grazed areas. Efforts to improve conditions for this species should be given long periods of time to be effective. The exclosures established for this study should be left in place for detection of longer-term effects of fencing on this species. To acquire additional long-term information, the study plots should be resampled at 3-5 year intervals.

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INTRODUCTION

Snake River goldenweed (*Haplopappus radiatus*) (Figure 1), is listed as a Bureau of Land Management (BLM) Special Status Species. In addition, it is listed by the Oregon Department of Agriculture as Endangered, and it is a Species of Concern with the U.S. Fish and Wildlife Service (Oregon Natural Heritage Program 2001). Most known populations are on land managed by the BLM in Oregon and several populations also occur in Idaho. Previous studies have clarified taxonomic problems with the species, located additional populations, described the identity and role of seed predators, and investigated the breeding system of the species (Kaye et al., 1990; Kaye and Meinke, 1992). However, little is known about its population dynamics and long-term trends. In addition, the effect of cattle grazing on Snake River goldenweed populations is unknown. This information is crucial for adequate management of the species.

Livestock grazing in the west is widely recognized as a management activity that may have negative effects on native species (Fleischner 1994, Cole and Landres 1996), including threatened and endangered plants (Schemske et al. 1994). Because of a joint interest in protecting Snake River goldenweed, the Oregon Department of Agriculture and the BLM Vale District entered into a cooperative project to determine long term population trends and identify factors that influence and control population growth. This work was continued as a challenge cost share project between BLM and the Institute for Applied Ecology. Previous reports have reviewed pertinent aspects of the species' biology and population monitoring techniques, and some of that information is repeated and updated here for completeness. This report represents a summary of the eleventh and final year of population monitoring, and presents evaluations of plant responses to cattle use, effects of precipitation and herbivory by grasshoppers on the species, discusses long-term patterns of seed predation by insect larvae, and presents computer models of Snake River goldenweed population dynamics.

Range

Haplopappus radiatus is narrowly endemic to the dry, rolling hills near the Snake River in eastern Oregon and adjacent Idaho (Figure 2). The global distribution of the species covers an area less than 30 x 40 miles. In Oregon, it occurs primarily in Baker County, and to a lesser extent in Malheur County, with many populations centered around the town of Huntington.

Reproductive biology

Snake River goldenweed (also known as *Pyrrocoma radiata*) blooms in June and July, rarely as late as September. The flowers are typically cross-pollinated by a diverse assemblage of bumble bees, solitary bees, flies, and butterflies. Some self-pollination is successful, but insects are required for maximum seed set (Kaye and Meinke, 1992). Weevils and other seed predators have been observed at several sites (Kaye et al., 1990). The exact timing of seed germination is unknown, but germination trials at Oregon State University indicate that seeds are germinable within a few weeks of dispersal, can germinate at temperatures at least as low as 7 °C, and some seeds will continue to germinate through fall, winter, and spring if kept moist (Kaye and Meinke, unpub. data). Seedlings (Figure 1) are present in the study populations as early as May (Kaye and Meinke, 1992). Snake River goldenweed is an herbaceous perennial from a woody tap root. As vegetative reproduction has not been observed in this species, seed production is considered to be vital for population growth.

Taxonomy and origin

Haplopappus radiatus is most closely related to *H. carthamoides,* a similar species of smaller stature in the subgenus *Pyrrocoma.* Some taxonomists elevate the subgenus *Pyrrocoma* to generic status, making *Pyrrocoma radiata* a synonym of *H. radiatus.* While *H. carthamoides* is usually diploid (n=6), *H. radiatus* is a hexaploid (n=18) with three times the number of chromosomes. One population of *H. carthamoides* var. *cusickii* that was studied by Kaye et al. (1990) was tetraploid (n=12), supporting the hypothesis that *H. radiatus* is an autohexaploid that resulted from a cross between diploid and tetraploid *H. carthamoides,* followed by a chromosome doubling event. A key distinguishing *carthamoides* and *radiatus* is available in Kaye et al. (1990), but more recent collections in Idaho by Michael Mancuso have not keyed easily in this treatment, suggesting that new morphological characters to distinguish the taxa need to be investigated, and/or that our current taxonomic understanding of the group is inadequate.

Habitat

Plants occur on dry, rocky, open soil generally on south to west-facing hillsides of gentle to steep (>50%) slopes (Figure 1). Elevations of reported sites range from 2100 to 6000 feet. The distribution of the species appears to be tied to a particular soil type, which is slightly to very calcareous, and often overlays a shale formation. The habitat of Snake River goldenweed is usually represented by a grazing-modified version of a sagebrush/grassland (*Artemisia tridentata/Agropyron spicatum-Poa sandbergii)* community. Associated species may include *Achillea millefolium, Agropyron spicatum, Amsinckia tessellata, Artemisia tridentata, Astragalus cusickii, A. purshii, Balsamorhiza sagittata, Bromus tectorum, Cardaria draba, Chrysothamnus nauseosus* var. *albicaulis, C. viscidiflorus, Collomia linearis, Crepis occidentalis, Elymus cinereus, Erigeron pumilus, Eriogonum compositum, E. elatum, E. microthecum, E. strictum, Erodium cicutarium, Gutierrezia sarothrae, Helianthus annuus, Mentzelia laevicaulis, Penstemon speciosus, Poa sandbergii, Purshia tridentata, Sisymbrium altissimum, Sitanion hystrix, Sphaeralcea munroana, Taeniatherum caput-madusae,* and *Tetradymia canescens.* The average annual precipitation in the area is 20-30 cm. All populations of the species fall within the Blue Mountains physiographic province (Franklin and Dyrness, 1973).

Objectives

The specific objectives of this report are to:

1. Document the effects of cattle grazing on populations of Snake River goldenweed by examining plant size and reproduction, population viability as described by demographic models, and interacting effects of climate and cattle usage on reproduction and population dynamics.
2. Evaluate the importance of environmental factors, such as precipitation and herbivory by grasshoppers, for plant and population growth.
3. Describe the interaction of predispersal seed predators (insect larvae) with each other and Snake River goldenweed.

Figure 1. Line drawing of Snake River goldenweed (*Haplopappus radiatus*) (left, from Hitchcock, et al. (1955), and photographs (right) of the flower, seedlings, and habitat (at Upper Lime exclosure).
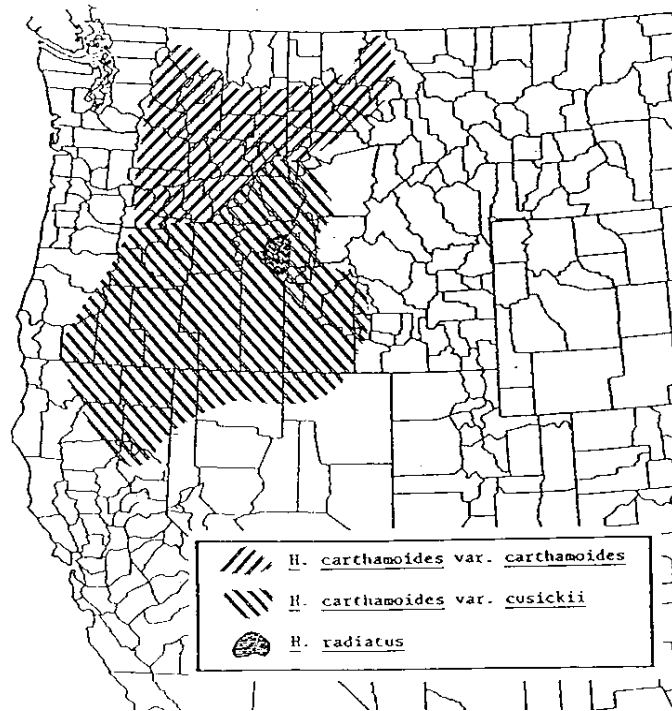
Figure 2. Distribution of *Haplopappus carthamoides* var. *carthamoides, H. carthamoides* var. *cusickii,* and *H. radiatus* in the western United States. Adapted from Mayes (1976).

METHODS

Study design

Five plots open to grazing were paired with fenced plots at sites within the Oregon portion of the range of Snake River goldenweed. All plots were established in 1991, and fencing was completed prior to the 1992 growing season. Plots were assigned to a fenced or unfenced treatment by a toss of a coin. Fenced areas are approximately 0.015 hectare, or 12 m on a side. The plots provide data on long-term population trends and the effect of cattle grazing on population growth. The sampling procedure is detailed enough to follow individual plants from one year to the next in order to determine the annual survivorship of individuals and identify the major reproductive- or size-classes in which plants can be categorized. The data are compatible with statistical methods and transition matrix models to determine population growth rates and other measures of population dynamics (e.g., Menges 1986, Caswell 2001), and comparisons of grazed and ungrazed plots.

Plot locations

A total of ten plots were established at four locations in the vicinity of Lime and Lookout Mountain Road in Baker County, Oregon. Plots are numbered 1-in, 1-out, 2-in, 2-out, and so on, with "in" indicating the plot is inside the exclosure, and "out" indicating the plot is outside the exclosure. Descriptions of the site locations and the plots are as follows:

> **Upper Lime (site 1)**: This site is located on a south-facing slope at 2000 feet elevation in an unnamed tributary drainage of the Burnt River, about 3/4 air mile northwest of Lime, T13S R44E S27 SW1/4 NW1/4. The site is best reached by taking the Lime exit off Highway 84 south-bound, and turning right (west) across the railroad tracks and through a gate (north of the over-pass). This dirt road doubles back north for about ½ mile then climbs west in the direction of Table Rock. Where the road begins to climb it may be impassable in wet weather, and the plot must be reached by foot. In either case, continue to follow the road up-hill for about ½ mile, then drop down (southeast) to the site. Two plots (1-in & 1-out), one inside and one outside of an exclosure, are located at this site. The fenced plot is below the unfenced plot. The Lower Lime site can be reached by continuing downhill from this site about ½ mile.

> **Lower Lime (site 2)**: This site is located on an east-facing, gentle slope at 2480 feet elevation with high shrub cover (*Artemisia tridentata*), about ½ air mile north of Lime , T13S R44E S27 SW1/4 NE1/4. It is about ½ mile below (east) of the Upper Lime site. To reach the site, take the Lime exit of Highway 84 south-bound and turn right (west) across the railroad tracks and through a gate (before the over-pass). This site can be reached either by driving on to the Upper Lime site and dropping down (east), or by parking among the trees just after crossing the railroad track, and walking uphill (southwest) to the site. Two plots (2-in & 2-out), one inside and one outside of an exclosure, are located at this site. The fenced plot is located southeast (and downhill) from the unfenced plot.

> **Upper Lookout (site 3)**: This site is located about ½ air mile northeast of the Lower Lookout site (see below) on a gentle, west-facing slope below the Lookout Mountain

Road, T12S R44E S33 NE1/4 SE1/4. Elevation here is 2960 feet. The site is reached by following the directions to the Lower Lookout site, continuing past this site about 3/4 mile along the Lookout Mountain Road, and parking at a pullout by the next cattle guard. There are two plots at this site (3-in & 3-out), one inside the exclosure, and one outside. Plot 3-out is located west (downhill) from plot 3-in.

Lower Lookout (sites 4-5): This site is located about 2 road miles south of Weatherby off Highway 84 along the Lookout Mountain Road, on a west-facing slope at 2720 feet elevation, T12S R44E S33 SW1/4 SE1/4. To reach the site, take the Lookout Mountain Road exit off Highway 84, and drive east on this road approximately ½ mile to a pullout at a cattle guard. The site is up-hill (north) of the road. Four plots (4-in, 4-out, 5-in, & 5-out), two inside and two outside of exclosures, are located at this site. Plot 4-in (with fence) is located northeast of plot 5-in (also fenced). Plot 4-out is northwest of 4-in, and 5-out is east of 5-in.

Plot set-up

All plots, whether inside or outside of an exclosure, were 10 x 10 m square and followed the same basic form. It was necessary to incorporate walk-ways into the plot set-up in order to reach the individual subplots for close inspection. Therefore, each plot was composed of five 1-m wide belt transects alternating with 1-m wide walk-ways (see Figure 3). The belt transects were marked permanently with rebar posts anchored at each end. Each transect was broken into 10 contiguous 1 x 1 m subplots in which plants were mapped and measured. Thus, there were five transects of ten subplots each, for a total of fifty subplots per plot (plot 1-out was an exception, with only 25 subplots, see "Sampling"). To locate the plots for sampling, a meter tape was run from the left post to the right post (left and right as if facing up-hill), and each 1-m segment of meter tape formed the lower edge of each subplot. A 1 x 1 m frame was then placed on the ground (with one edge along the meter tape) to delineate the subplot. Subplots were identified by means of a coordinate system in which transects were labeled as A through E and subplots as 1 through 10. For example, the fourth subplot from the left in transect D was subplot "D-4" (see Figure 3).

Table 1. Summary of site and plot names and numbers.

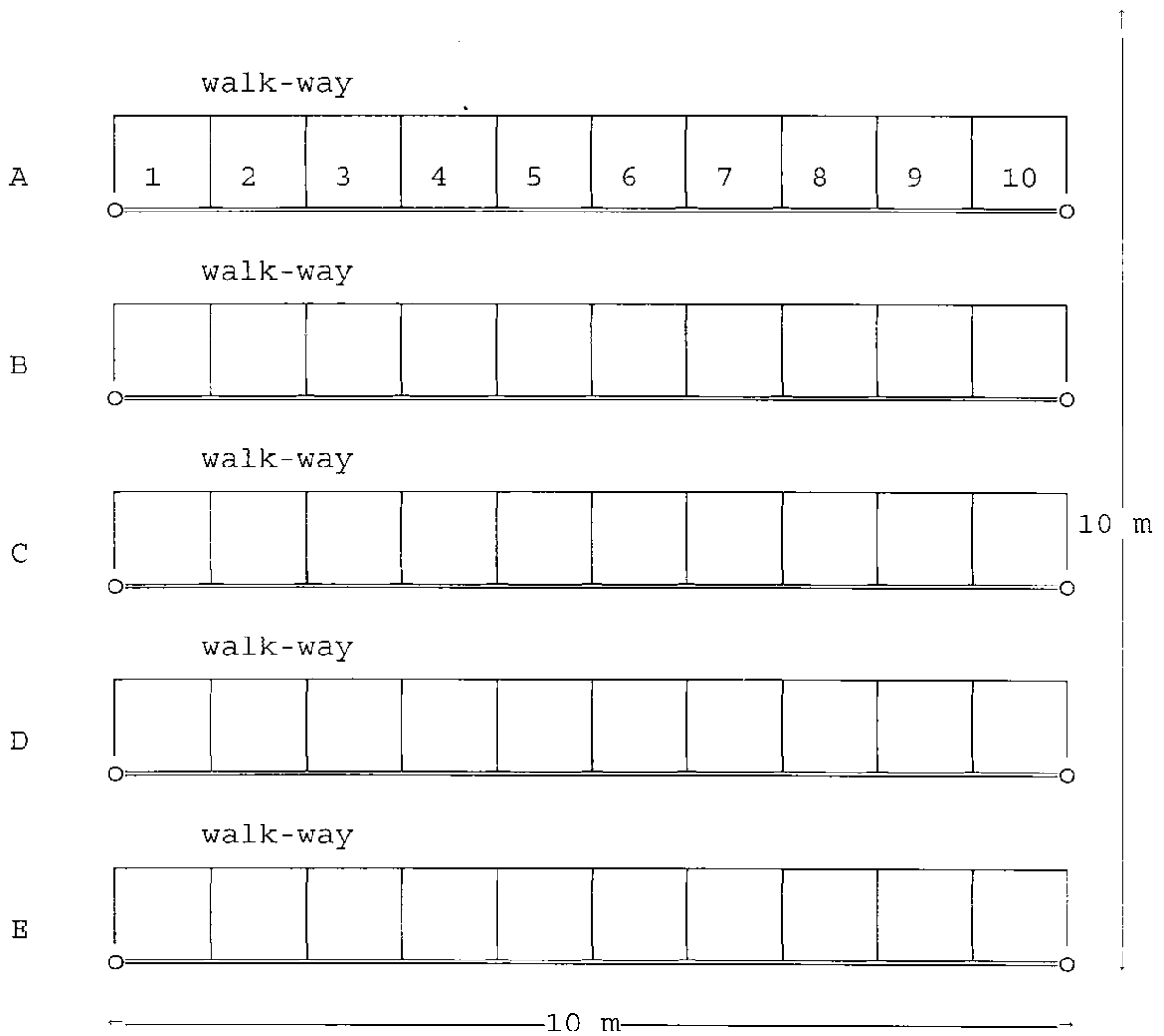| site name	site number	plots[*]	
Upper Lime	1	1-in & 1-out	*"in" and "out" refer
Lower Lime	2	2-in & 2-out	to inside and outside of
Upper Lookout	3	3-in & 3-out	cattle exclosures
Lower Lookout	4 & 5	4-in & 4-out, 5-in & 5-out	

Figure 3. Layout of permanent plots for monitoring Snake River goldenweed. Plots were 10 x 10 m, and composed of five parallel belt transects (A-E), each 1 m wide, separated by a 1 m walk-way. Each transect was divided into ten consecutive 1 x 1 m subplots (1-10). Transect endpoints were marked permanently with rebar posts (marked "o").

Sampling

In each year from 1991 through 2001, sampling was conducted twice, once in mid-May and once in late-July or early August. The spring samples were conducted primarily to maintain the plots and locate and map seedlings. All plants were measured and remapped during the summer sample. In every subplot, all Snake River goldenweed individuals were mapped onto special map forms and numbered consecutively on the map. Data on plant height (cm), length of longest leaf (cm), number of leaves, number of healthy and aborted flower heads (capitula), number of grazed stems, and percentage herbivory by grasshoppers, were recorded onto a second data sheet. In 1991, at the beginning of the study, the density of Snake River goldenweed was so high at the Lime sites (1 & 2) that we reduced the area of the subplots where non-reproductive plants are mapped and measured to the lower left-hand quarter of the subplots. All reproductive individuals in the entire subplot were mapped and measured in the Lime plots (1 & 2). In addition, only even numbered subplots were sampled at Upper Lime plot 1-out. All portions of all subplots were sampled at the Lookout Mountain Road sites (plots 3, 4 & 5). In 1996, protocol was changed at the Lime sites so that mapping and measuring included all plants in all plots (not just the lower left corner of some plots).

Determination of seed production and predation

At each of the four sites, entire seed heads were collected at random to determine the number of seeds matured (healthy and filled), damaged (eaten by insects), and aborted. In each case, the insect(s) responsible for damaging seeds were identified, if possible, to the three major insect types: weevil, cecidomyiid midge, and gelechiid moth larvae (Figure 4). Seed heads were gathered along temporary transects adjacent to the plots. The seed heads were dissected, and the number of seeds in each category were counted. This information was used to estimate the number of healthy seeds produced by each plant by multiplying seeds/capitulum by non-abortive capitula/plant within each site. Estimates of seed production were made every year except 1993 (because flowering was late that year and sampling occurred while the plants were still in flower).

Analysis

We used a Wilcoxon signed-rank procedure to test for a significant difference in plant size (length of longest leaf and plant height) and reproduction (number of healthy flower heads per plant), between grazed and protected plots in all years (n=5 pairs of plots). An α-level of 0.1 was set prior to the analyses for rejection of the null hypothesis of no effect.

We also examined correlations of environmental variables and plant response variables to develop explanatory models of Snake River goldenweed and grasshopper herbivory (Table 2). We used stepwise multiple regression to build these correlation models. Seasonal precipitation was an important climatic variable included in many regression models. We obtained precipitation records from the nearest weather station for which relatively complete records were available, Baker City Airport, and, where data gaps occurred in this data set, we filled them with rainfall values from Huntington, Oregon. These records were obtained from the Oregon Climate Service website. Monthly precipitation amounts for each year of the study were combined into seasonal precipitation measures as follows: fall (October through December), winter (January-March), spring (April-June), and summer (July-September). Models were considered significant at the α=0.1 level of probability.
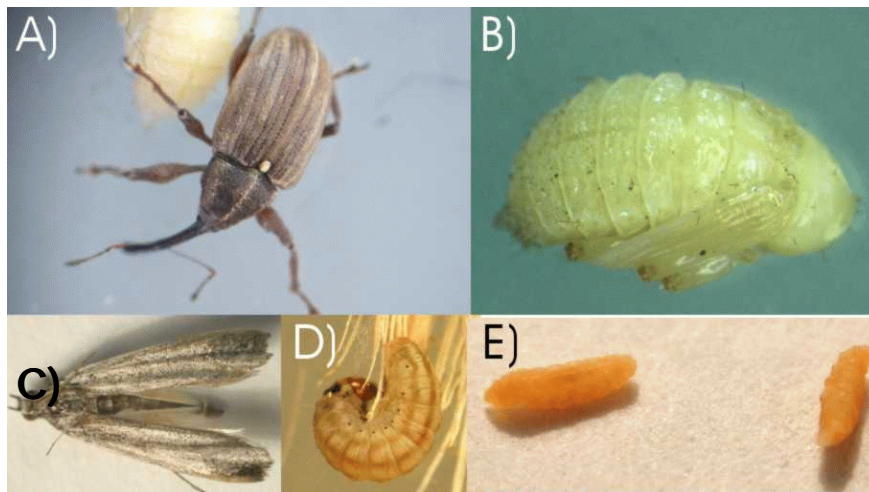
Figure 4. The major insects that damage seeds in the flower heads of Snake River goldenweed include weevils (A–adult, B–pupa), gelechiid moths (C–adult, D–larva), and cecidomyiid midges (E–larvae).

Table 2. Plant response variables and independent variables examined in stepwise multiple regression to develop explanatory models for Snake River goldenweed.

Variable	Independent variables examined in stepwise regression
seed production	precipitation (fall, winter, spring, summer), frequency of grazing, grasshopper herbivory
seed predation by insect larvae	precipitation (fall, winter, spring, summer), frequency of grazing, grasshopper herbivory
flower head production	precipitation (fall, winter, spring, summer), frequency of grazing, grasshopper herbivory
seedling establishment	healthy flower head production in the previous year, healthy seed production per head in the previous year, precipitation (fall, winter, spring, summer), frequency of grazing in the previous year, grasshopper herbivory in the previous year
population growth rate (λ)	healthy flower head production in the previous year, healthy seed production per head in the previous year, precipitation (fall, winter, spring, summer), frequency of grazing in the previous year, grasshopper herbivory in the previous year
grasshopper herbivory	precipitation (fall, winter, spring, summer)

The matrix model of population dynamics

Population model

Populations from each study site were modeled with a transition matrix approach. This type of model is based on the reproduction and survival of individuals. For the purposes of the model, the individuals in a population are divided into categories based on age, size, or life-history stage. Then, the number of seedlings produced per plant in each category is determined, and the probability that an individual will survive in the same stage or make the transition from its current category to another must be calculated. The "transition probabilities" are merely the proportion of individuals in each stage that "make the transition" to another stage (e.g., become smaller or larger) from one year to the next. Figure 5 is a life-cycle graph for Snake River goldenweed with four possible

Figure 5. Life-cycle graph of *Haplopappus radiatus*. **S**= seedlings, **J**= juveniles, **V**= vegetatives, and **R**= reproductive plants. Each arrow represents a possible transition (or reproduction) pathway from one year to the next. Small-curved arrows allow for plants to remain in the same stage; double-ended arrows indicate plants may go back and forth between stages.

stages: seedling (S); juvenile (J), ≤three leaves; vegetative (V), ≥4 leaves and non-reproductive; and reproductive (R). The arrows indicate the possible transitions (or fecundities, lowest arrow) that plants in each category can make as one year passes.

Below is the stage-classified transition matrix for *Haplopappus radiatus* based on the life-history graph (Figure 4), and a population vector, which contains the number of plants in each category. The matrix contains four categories (S through R). Plants in each category can make the transition from their current condition to the same or another class the following year.

Transition matrix:		S	J	V	R		*Population vector:*	
	S	--	--	--	F_{R-S}			n_S
	J	G_{S-J}	P_{J-J}	G_{V-J}	G_{R-J}			n_J
A =	V	G_{S-V}	G_{J-V}	P_{V-V}	G_{R-V}	**n** =		n_V
	R	G_{S-R}	G_{J-R}	G_{V-R}	P_{R-R}			n_R

In this transition matrix (**A**), the number of seedlings produced per year per individual (fertility) in each category is represented by **F** in the top row. The probability that a plant in a particular category will persist in the same category the following year is indicated by **P**; these probabilities are found along the diagonal of the matrix. Finally, plants have a probability **G** of growing into a new category the following year. For example, reproductive plants produce F_{R-S} seedlings per year, they have a probability P_{R-R} of remaining in category R, and probabilities G_{R-J} and G_{R-V} of making the transition to the juvenile or vegetative stages, respectively. Notice that plants can regress from a larger category to a smaller one, and that small plants can grow

to larger plants more than one size class above them. This type of matrix is a Lefkovitch matrix (Lefkovitch, 1965), which is a generalization of an age-based (or Leslie) matrix (Leslie, 1945). For plants, the age of an individual is often difficult to determine or not very meaningful. For example, many herbaceous perennials do not form annual growth rings the way trees do, and even if they did, age does not necessarily relate to a plant's size or ability to reproduce. Moreover, the process to determine plant age may require its destruction, a method that is clearly inappropriate for rare plants. Instead, most models of plant populations place individuals into size or stage classes, or a combination of the two, as was done here. The number of individuals in each category n_i is found in the population vector (**n**). The transition matrix is post-multiplied by this population vector to project the total population in time. Each time the model is iterated in this way, a single time step (one year) is completed.

Population growth rate
We used two different approaches to model the populations. The first approach was to calculate a measure of population growth, lambda (λ), for each plot at each site. Lambda is the equilibrium population growth rate (and the primary eigenvalue of the transition matrix), and can be used as a single measure of population viability to compare sites and treatments. If lambda is less than 1.0 the population will be projected to decrease in size (a non-viable population). If lambda is greater than 1.0 the population will grow (a viable population), given that current conditions remain constant. For each site and treatment, we calculated lambda for pairs of consecutive years (1991-92, 1992-93, etc.). Unfortunately, adequate seedling survival data from many plots was not available to execute the model, especially in 1991-92. For example, in some plots, no seedlings survived at all, and in others, all seedlings survived. Also, in some plots, no reproductive plants were observed in some years, so no data were available to estimate transition probabilities of this stage class. Therefore, where data were lacking, we used the average of transition probabilities from the years when these data were available. This process allowed us to calculate lambdas and elasticities for matrices where we otherwise would not have been able to. We also calculated the stochastic growth rate (λ_s) for each plot. This measure of population growth has fewer assumptions and yields an average growth rate for the plot over the course of the study. Calculations of λ_s were based on simulations of 100,000 time steps.

Extinction probability
Our second modeling approach was to incorporate environmental variability (stochasticity) into our simulations to compare population dynamics under grazed and protected conditions. This kind of modeling involves projecting future population dynamics by randomly selecting survival and fecundity measures from past years. We included environmental variability in our model through the matrix selection method. Matrix selection involves selecting at random one of several available transition matrices with equal probability at each time step. The matrices represent each year of the study, and the variation between them is considered to be environmental stochasticity. More detailed descriptions of this method can be found elsewhere (e.g., Burgman et al., 1993). We used the program SHUFFLE (Kaye, unpublished program) written for MATLAB to implement the models. All simulations ran for 50 years and consisted of 1000 iterations, which allowed us to determine an average projected population trend. The starting population size for each simulation was 1000 plants distributed among the four stages with the relative abundance representative of the average structures for each plots over all years. The simulations stopped at the quasi-extinction threshold of 10 individuals; this provides a conservative estimate of extinction dynamics.

Assumptions of the model
Our use of the transition matrix model assumes that fertility and transition rates are independent of plant density. This is an acceptable assumption for many species with population densities below the density-dependent threshold (density-vague populations). In addition, the model assumes that population growth is a first-order Markov process, where the probability that a plant will change in size next year is independent of its size in the previous year. And finally, for deterministic modeling (calculation of non-stochastic lambda), transition rates are assumed to remain constant in time.

Analysis
We used MATLAB to assist in the construction and iteration of our models. This commercially available computer software program makes implementation and alteration of the models a standardized task. The software allowed us to calculate annual population growth rates (lambda, λ), and, for the stochastic models, stochastic growth rates (λ_s) and extinction probabilities as measures of population viability. Stochastic growth rate and extinction probability were compared using a Wilcoxon signed rank test. Annual measures of λ were correlated with precipitation variables, frequency of grazing, grasshopper herbivory, flower head production, and seed production in stepwise multiple regressions, as above for other plant responses.

RESULTS

Effects of excluding livestock

Grazing intensity

Grazing impacts on Snake River goldenweed varied substantially from year to year at the study sites. The average frequency of grazing on the goldenweed in unfenced plots varied from 0.2% in 1993 to 16% in 1994, and often alternated between heavy and light grazing from year to year (Figure 6). The frequency of grazing on Snake River goldenweed was significantly higher in unfenced plots than fenced plots in 1992, 1996, 1998, 2000, and 2001. Some grazing on Snake River goldenweed plants occurred even inside the exclosures, and this was attributed to deer and rabbits that were able to get over or through the fences, and to cattle

Figure 6. Mean frequency of cattle grazing on Snake River goldenweed from 1991 through 2001. Significant differences (*P*<0.05) in each year between fenced and grazed plots denoted with an asterisk (*).

that leaned against the fences and reached the outer plants in the plots. In most years, this amounted to a background level of grazing ranging from 0 to 2%, except in 1994 when the frequency of grazing reached 13% inside the exclosures. Therefore, the exclosure fences were generally effective at protecting Snake River goldenweed and its associated habitat from cattle herbivory, and presumably, trampling.

Plant size and reproduction

Snake River goldenweed plants inside exclosures were significantly larger and produced more flower heads than plants in unfenced plots in the later years of this study. From 1991 through 1996, for example, no significant differences in plant size or reproduction were detected, but from 1997 through 2001, the length of the longest leaf in grazed plots was significantly shorter than in protected plots (Figure 7). By 2001, longest leaves in grazed plots averaged 14.4 cm, while those inside exclosures averaged 22.1 cm, a difference in size of nearly 35%.

Plant height was also significantly lower in grazed plots in 1999–2001, averaging 45% of the height of plants inside fences in 2001. Plants in unfenced plots produced significantly fewer flower heads than those in protected plots in 1999 and 2001. In 2001, the average plant in grazed plots produced only 0.15 heads, while protected plants yielded 2.3 flower heads (Figure 7).

Figure 7. Mean length of longest leaf (top), plant height (center), and number of flower heads per plant (bottom) for Snake River goldenweed in fenced and grazed plots from 1991 through 2001. Significant

differences (*P*<0.05) between protected and grazed plots are denoted with an asterisk. Exclosures were fully installed prior to the 1992 growing season.

Population growth rate

Population growth rate (lambda) was affected by fencing treatments only in 2000, nine years after fences were installed (Figure 8). In that year, the average population growth rate in protected plots was 0.893, while in grazed plots it was 0.728, a difference that was statistically significant (*P*=0.04). However, this effect was not detected in any other year.
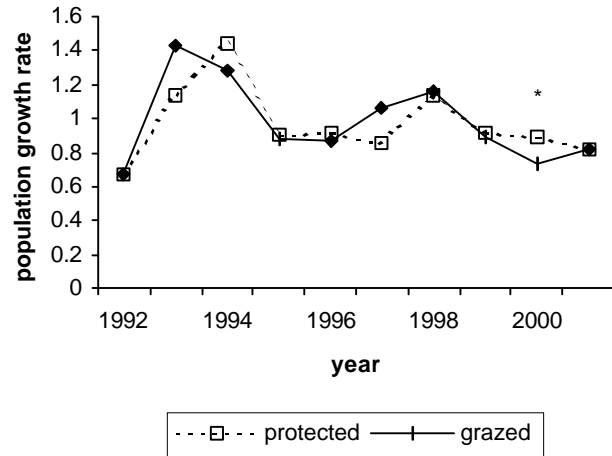
Population viability

Both measures of population viability explored in this study showed no significant difference between fenced and unfenced populations. Average stochastic population growth rate was nearly identical (approximately 0.97) under both treatments (Figure 9, top). Mean extinction probability was also very close under both treatments at 42% vs. 36% for protected vs. grazed populations, respectively (Figure 9, bottom).

Figure 8. Snake River goldenweed average population growth rates in fenced and grazed plots from 1991 through 2001. A growth rate >1.0 indicates a growing population, while a growth rate <1.0 indicates decline. A significant difference (*P*<0.05) between protected and grazed plots in 2000 is denoted with an asterisk.
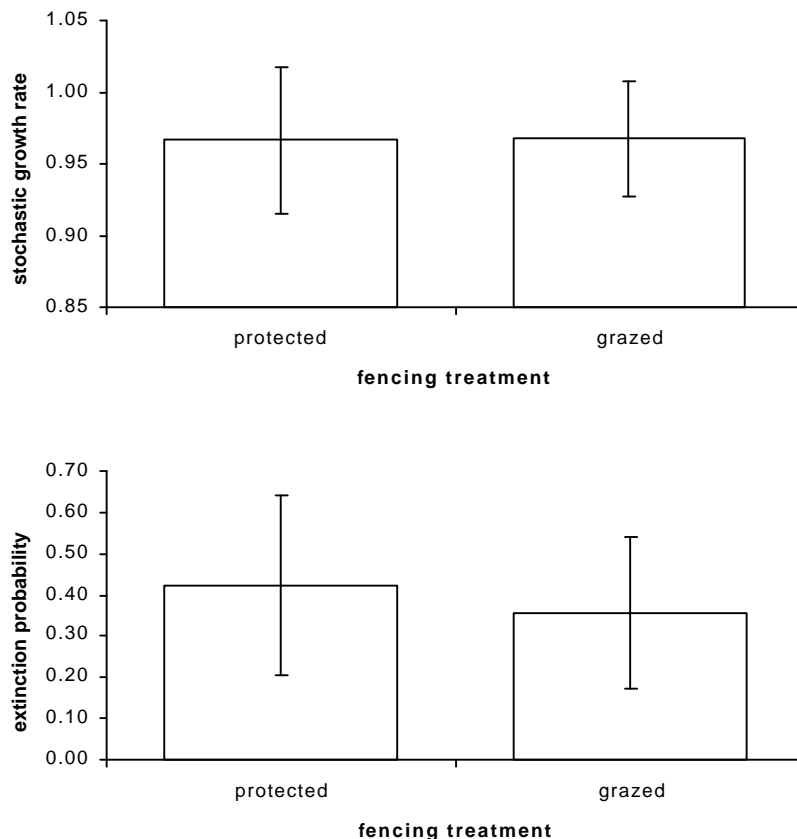
Figure 9. Two measures of population viability for Snake River goldenweed in fenced and grazed plots. Stochastic population growth rate (top) is a measure of growth rate in a variable environment, while extinction probability (bottom) quantifies the risk of catastrophic decline. In this case, extinction probability was defined as the risk of falling below ten individuals in 50 years. No significant differences were detected between protected and grazed plots for either variable. Vertical lines represent ±1 standard error.

General population dynamics – ***Population summary***

Between 1991 and 2001, a total of 16,041 plants were mapped and measured in all plots combined. The majority of these plants were seedlings that lived for only one or two seasons, then died without becoming reproductive. Plant density varied widely from site to site and plot to plot. In general, average plant density was greatest at the Lime sites, especially in plot '1-in' at Upper Lime (e.g., 46.7 plants/m^2 in 1994). Density was lowest at the Lower Lookout sites, especially in plot '5-out' (e.g., 0.38 plants/m^2 in 1994), reflecting the differences in overall habitat quality – and possibly grazing history – at these sites. The abundance of reproductive plants was greatest at the Upper and Lower Lime over all years of the study, and lowest at Lower Lookout (plots 4 and 5) (Figure 10). In general, the number of reproductive plants in the study plots has varied substantially since 1991, and, at the Lime sites, showed overall declines.

In general, Snake River goldenweed density, height, number of leaves, length of longest leaf, number of flower heads, and number of seeds per plant were greater at the Lime sites (1 & 2) than the Lookout sites (3, 4, & 5) in all years of this study. Plants at site '2-in' at Lower Lime consistently produced significantly more seeds than plants in any other plot (e.g., 356 seeds/plant in 2000 and 375 seeds/plant in 1995 compared to 0-100 for most other sites). No information on seed production is available for 1993 because field sampling occurred while the plants were in flower.

Grazing was heavy near site 2, where moisture is available at a nearby spring. Although the plants in the exclosure are protected from this herbivory, they have faced potential competition from the invasive plant, *Cardaria draba* (white-top), which is threatening to become a dominant species inside the exclosure.

Population structure

All Snake River goldenweed populations within the plots were dominated, on average, by small plants (seedlings or juveniles), both inside and outside of the fences (Figure 11). At Upper Lime, both plots were dominated by seedlings, with lesser amounts of juveniles, vegetatives, and reproductive plants (ranked in that order). Also, the fenced plot at Lower Lime was dominated by seedlings, and the non-fenced plot at Upper Lookout was dominated by vegetative plants.
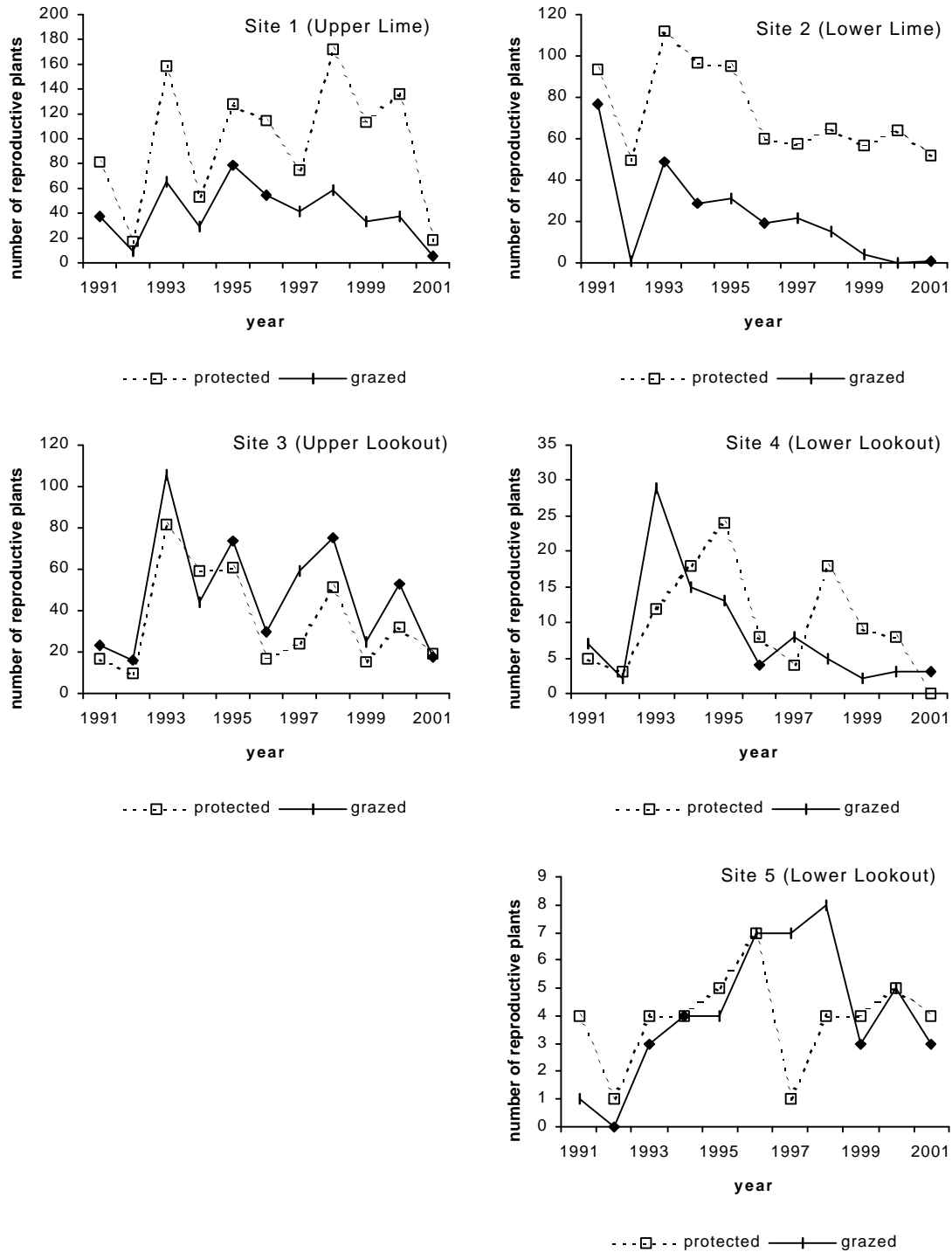
Figure 10. Number of reproductive Snake River goldenweed plants in protected (fenced) and grazed plots at five study sites from 1991 to 2001.
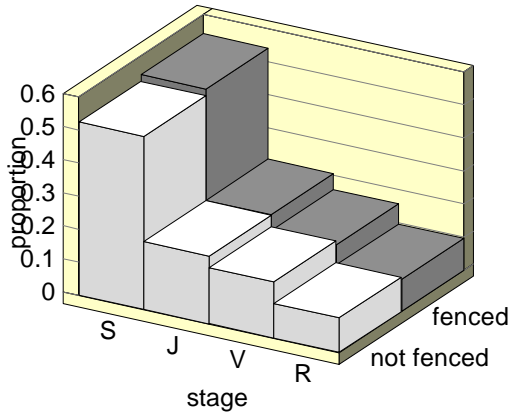
site 1 (Upper Lime)
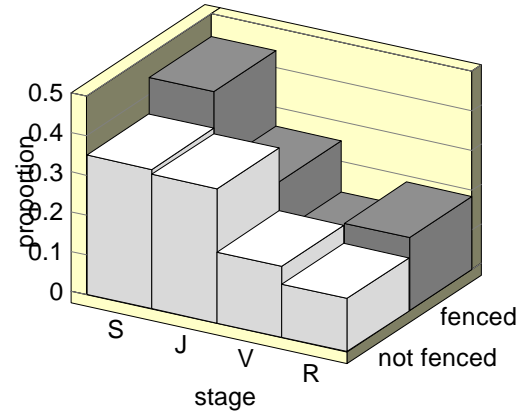
site 2 (Lower Lime)
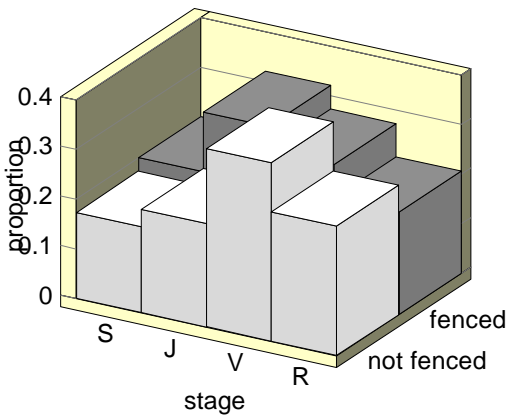
site 3 (Upper Lookout)
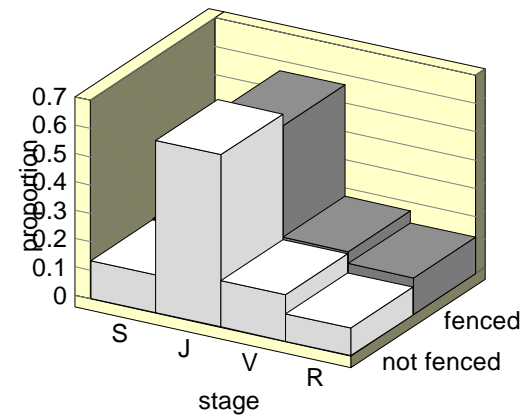
site 4 (Lower Lookout)

Figure 11. Average population structure of Snake River goldenweed at five study sites from 1991-2001, inside and outside exclosures.
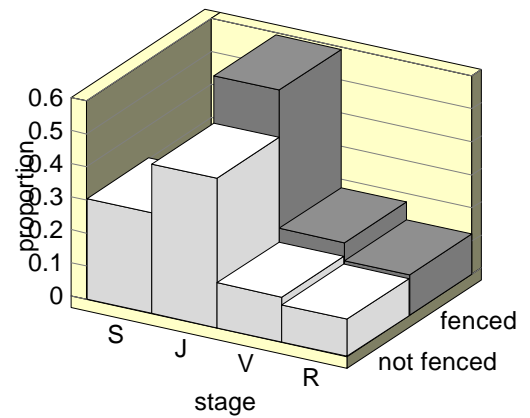
site 5 (Lower Lookout)

Environmental factors affecting Snake River Goldenweed

Factors affecting seed production

Summer precipitation and herbivory by grasshoppers were identified by stepwise multiple regression as the best explanatory variables of mean seed production in Snake River goldenweed. A total of 78% of the annual variation in the proportion of healthy seeds set in each head was explained by summer precipitation (July through September, P=0.034) and intensity of tissue damage by grasshoppers (P=0.095). Summer precipitation had a positive effect on seed set, while grasshopper damage had a negative effect. The total number of seeds produced per flower head was positively correlated with summer precipitation, which accounted for 67% of its variation (P=0.0023, Figure 12).

Seed predation by insect larvae was also affected by precipitation. Winter (January-March) precipitation was negatively correlated with mean percentage seeds damaged by insects (P=0.0499), and this factor explained 33% of the variability in seed predation (Figure 13).
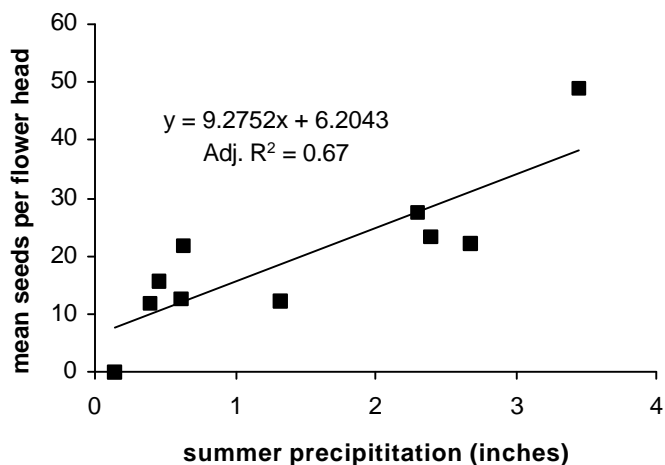
Figure 12. Relationship between average seed production

$y = 9.2752x + 6.2043$
Adj. R^2 = 0.67
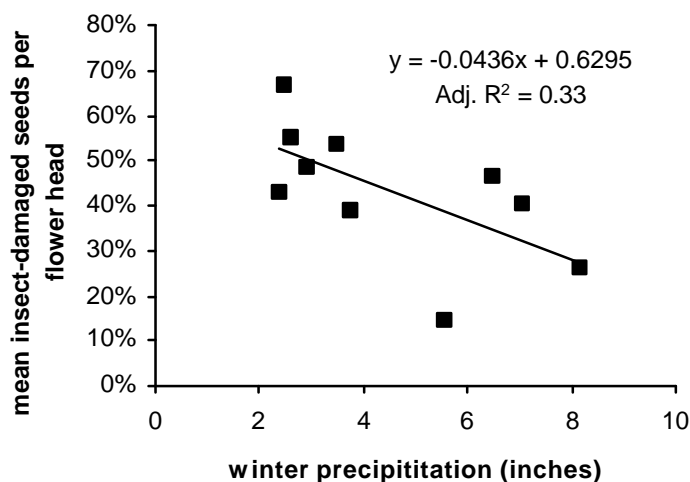
Figure 13. Relationship between average seed predation in Snake River goldenweed and winter (January-March) precipitation.

$y = -0.0436x + 0.6295$
Adj. R^2 = 0.33

Factors affecting flower head production

Flower head production in Snake River goldenweed appeared to be a function of climate and frequency of herbivory by cows (Figure 14). In unfenced plots, winter precipitation (January-March) had a positive effect on flower head production, the frequency of herbivory had a negative effect, and together these variables explained 76% of the variability in flower head production (P=0.0013).

In fenced plots, cattle utilization was not a significant variable, and only winter precipitation was brought into the model by stepwise regression. Winter precipitation explained 62% of the variability in flower head production in fenced plots (P=0.0024) (Figure 14).

Neither herbivory by grasshoppers nor any other precipitation variables were significant factors in these regression models.
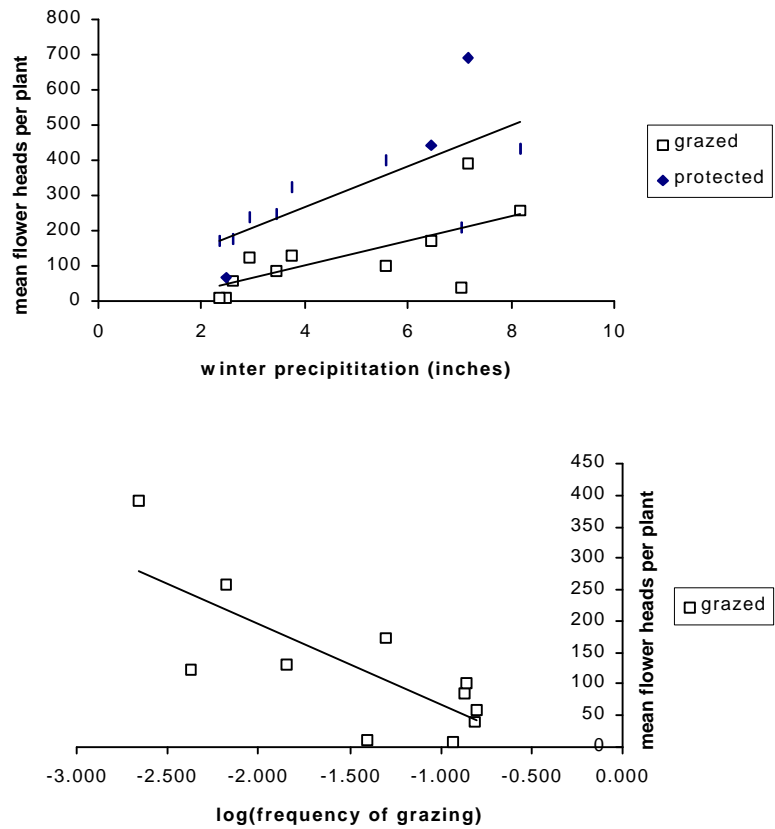
Figure 14. Relationship between flower head production in Snake River goldenweed and winter precipitation (top) and frequency of grazing (bottom).

Factors affecting seedling establishment

Mean seedling abundance was strongly correlated with the number of flower heads per plant in the previous year. In correlations with these variables, the log of the mean number of seedlings per plot in any given year was significantly associated with the number of healthy flower heads produced the year before in both grazed (P=0.0024, adj. r^2=0.667) and protected (P=0.0339, adj. r^2=0.380) plots. As the number of flower heads increased, the number of seedlings the following year also increased (Figure 15).
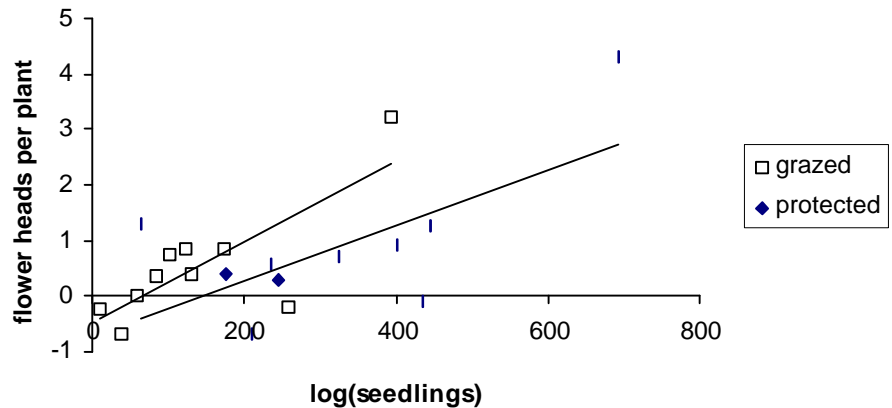
Figure 15. Relationship between seedling recruitment per plot and flower head production per plot in the previous year.

Factors affecting population growth

Average population growth rate (λ) was also correlated with climate and livestock use. In protected plots, fall (October through December) precipitation explained a significant portion of the variability in population growth rate (P=0.057, adj. r^2=0.303). As rainfall increased, so did population growth rate (Figure 16). In grazed plots, both fall precipitation and grazing frequency were correlated with population growth; λ was positively correlated with rainfall and negatively associated with log of frequency of livestock grazing (Figure 16). These two variables together explained 44% (adj. r^2) of the variability in population growth rate in grazed plots (P=0.056).
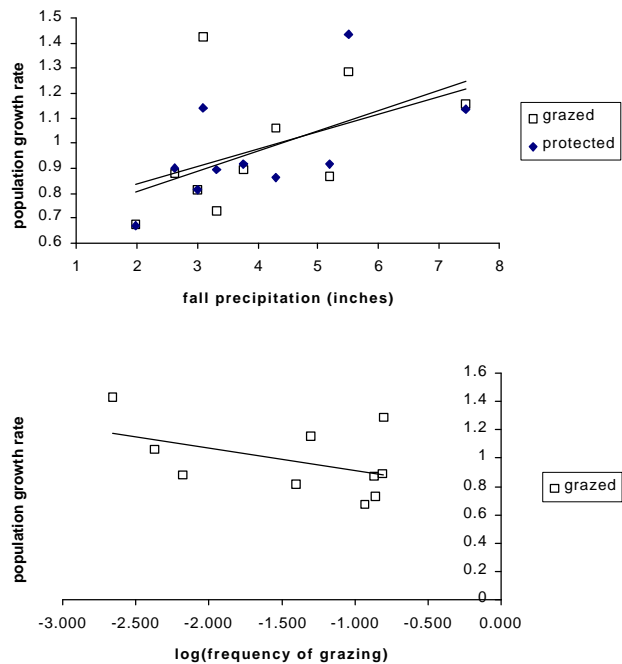
Figure 16. Relationship between population growth rate and fall (October-December) precipitation (top) and frequency of grazing (bottom).

Plant-insect interactions

Seed predation

Insect larvae in the flowers heads of Snake River golden weed damaged or consumed a substantial proportion of ovules in some years (Figure 17, top). Average seed predation varied from a low of 15% in 2000 to a high of 67% in 1992. As described above, this annual variation was correlated with winter precipitation, with more seed damage occurring after dry winters (Figure 13). Depredation by insect larvae was the greatest cause of seed loss in 1992, 1994, 1996, 1997, 1998, and 2001. In 1998, seed loss to insects was greatest at Upper Lookout (95.4 seeds per head) and lowest at Upper Lime (29.0 seeds), but note that this relative ranking has shifted each year since 1991. In 1999, abortion was the greatest cause of seed loss at all sites. In 1992, no measurements of seed production or loss were made at Lower Lookout because flowering was too infrequent at that site to provide a sample.

Seed loss to abortion has varied as well over the years of sampling, ranging from a high average of 70 seeds per head in 1991 and 87.8 in 1999 to a low of 22 seeds in 1992. Healthy seeds made up the smallest fraction of available ovules per head in all years except 1995. As noted above, in 1999, no healthy seeds were recorded at Upper Lime, Lower Lime, and Upper Lookout, and seed production at Lower Lime was less than 1 seed per flower head. The high rates of abortion in that year were probably due to stress caused by above average grasshopper herbivory. No data for seed losses are available for 1993. 2000 was a better than average year for seed production, with overall mean seed production exceeding 27 seeds per head.

Figure 17. Average seed predation by insects in flower heads (top) and leaf herbivory by grasshoppers (bottom) in each year since 1991 (seed predation data not available in 1993).

The primary seed predators encountered were weevil larvae, gelechiid moth larvae, and cecidomyiid midge larvae. These insects varied substantially in their frequency in our samples from year to year and site to site. When insect frequency data were pooled across all years and plots, chi-square tests indicated that these three species tended to avoid one another (*P*<0.0001, all tests). That is, although weevils could (and often did) occur in the same flower heads as other insect larvae, there was a tendency for them to occur in heads without these other insects, and vice versa.

Figure 18. Average seed predation by insect seed predators (weevil, midge, and moth larvae) alone and in combination. Data were pooled over all years and sites of the study. Error bars represent ± 1 standard error. Bars topped with the same letter do not differ statistically at the 0.05 level of probability.

The major insect seed predators encountered in this study differed in their effects on Snake River goldenweed seeds. When encountered in flower heads, weevil larvae damaged the most seeds ($\bar{x}$=59%), followed by moth larvae ($\bar{x}$=45%) and midge larvae ($\bar{x}$=33%) (Figure 18). When midge and moth larvae co-occurred in the same flower head, total seed predation ($\bar{x}$=57%) was significantly higher than when either were encountered alone. When these insects were found in heads together with weevils, however, total seed predation was not increased above levels where weevils were found alone (Figure 18).

Grasshopper herbivory

Average herbivory by grasshoppers was not affected by the exclosures, and ranged from a low of 11.5% in 1993 to highs of 61% in 1999 and 63% in 1994 (Figure 17, bottom).

Herbivory by grasshoppers differed among years, and was least prevalent after a dry fall. October-December precipitation significantly (P=0.065) explained 25% of the variability in grasshopper herbivory on Snake River goldenweed (Figure 19).
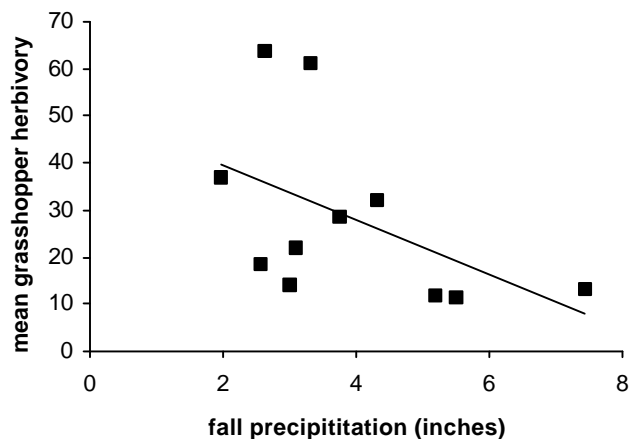
Figure 19. Relationship between grasshopper herbivory and fall (October-December) precipitation.

DISCUSSION

Effects of cattle grazing on Snake River goldenweed: plant size and population dynamics

We tested for effects of livestock grazing on Snake River goldenweed in three general ways: by examining effects on plant size over time, testing for effects on population viability, and measuring the importance and interaction of climate and grazing frequency on annual population growth rate. Fencing Snake River goldenweed to exclude livestock over a ten year period resulted in an increase in plant size and reproduction over unfenced plants, but this increase only became apparent after several years of protection. Leaves were significantly longer inside exclosures than outside after five years of protection, and plants were taller only after seven years (Figure 7). Flower head production was significantly higher inside exclosures than outside seven and nine years after fencing (Figure 7). No effects of excluding cattle were detected on population growth rate until the eighth year after fencing, but this effect was not detected the following year (Figure 8). Releasing Snake River goldenweed from grazing impacts by livestock clearly resulted in an increase in plant size and reproduction, but had only weak effects on population growth rate even after nine years of fencing.

Seasonal precipitation also had impacts on population growth rate, and this effect interacted with cattle usage. In both grazed and protected populations, fall precipitation increased population growth rate significantly. But in plots left exposed to livestock use, the frequency of grazing on Snake River goldenweed tended to reduce population growth rate (Figure 16). Therefore, these factors could interact with each other to affect goldenweed populations. For example, in years with high grazing frequency, when population growth might be expected to decline, if fall precipitation was also high the impacts of grazing could be partially counteracted. And by the same reasoning, if grazing frequency was low in a given year the population might still do poorly if this coincided with a dry fall. These two factors together accounted for 44% of the observed variation in population growth. Flower head production was also affected by climate (winter precipitation) and frequency of grazing, which together explained 76% of the variation on fecundity.

Estimates of population viability in Snake River goldenweed populations inside cattle exclosures did not differ from those for populations outside the fences. Average stochastic population growth rate was 0.97 in both fenced and unfenced plots, and the 95% confidence intervals for these estimates (0.82-1.11 and 0.86-1.08 for protected and grazed populations, respectively) overlapped 1.0, indicating that there is no evidence that the populations have been, on average, in decline. In addition, mean extinction probability (risk of falling below ten individuals in 50 years) for the populations did not differ inside or outside of the exclosures. These estimates were 0.42 (95% confidence interval 0-1) and 0.36 (0-0.89) in protected and grazed plots, respectively. Even so, it is possible that a more sophisticated modeling approach, one that combined precipitation and grazing into a single mechanistic model, might reveal more about the long term effects of cattle grazing on Snake River goldenweed.

A long history of cattle, sheep, and wild horses in the population areas (Kaye and Meinke 1992, Greenlee and Kaye 1995) appears to have led to degradation of the habitat, and although cattle use at the Lime and Lookout sites may be currently light, depending on the year, past uses have caused soil compaction and considerable changes in the associated vegetation. Grazing in arid rangelands has been shown to decrease plant species diversity in

sagebrush dominated habitats in Idaho (Reynolds and Trost 1980) as well as riparian areas in Oregon (Winegar 1977). Livestock grazing in the United States is a major threat to 22% of threatened and endangered species, and 33% of endangered plants alone (Wilcove et al. 1998). In Oregon, livestock grazing has been identified as the primary threat to 44% of the state's rare plants (Kaye et al. 1997). Grazing and trampling by livestock in the arid west has altered vegetation and habitats for many species and occurs over a substantial portion of the region (Dwire et al. 1999). Although studies of the effects of cattle grazing on rare plants are surprisingly few, those that have been conducted suggest that the impacts of grazing affect both rare species and their habitat. For example, the rare plant *Phlox idahonis* in north-central Idaho appears to decline under pressure from cattle grazing due to direct impacts on plants from grazing and trampling and indirect effects through a degradation of habitat and an increase in invasive plants (Moseley and Crawford 1995). Two rare plants in California are smaller in grazed habitats compared to non-grazed areas, and the cover of dominant woody species in their habitats also differ with grazing (Willoughby 1987). In the current study, Snake River goldenweed appeared to be impacted by livestock use at several stages, including plant size, flowering, and annual population growth.

Summary of population dynamics

Annual climatic variation in Baker County seems to have had a large influence on plant size, fecundity, and mortality; overall, plants were smaller in the drier years of 1992 and 1994, and larger during the wetter years of 1993 and 2000. Annual variation in climate seems to play a large role in population dynamics from year to year, with precipitation in different seasons affecting plants in different ways. For example, summer rainfall appears to be an excellent predictor of seed set in Snake River goldenweed, and flower head production is positively correlated with precipitation during the previous winter. And, as noted above, fall precipitation is positively associated with annual population growth rate.

Our analysis of over sixteen-thousand Snake River goldenweed individuals over an eleven-year period indicates that mortality is highest for seedlings, followed by juvenile, vegetative, and reproductive plants, regardless of grazing treatment. In other words, a plant's chances of survival improve as it increases in size, and perhaps age. In all years of the study, the populations we have observed differed from site to site in terms of density, plant size, and fecundity. Also, the structure of the populations has differed, with the populations at the Lime sites showing higher proportions of seedlings than other stages, on average, and the Lookout sites tending to have higher proportions of juvenile and vegetative plants. This difference may be due, in part, to greater flower head production at the Lime sites, which leads to higher seed production and resulting in large numbers of seedlings in many years. In general, differences between the sites in soil depth, fertility, soil chemistry, slope, aspect, grazing history, and associated species are the most likely causes of variation in average plant size and population structure.

Stochastic matrix projections using ten matrices from 1991-01 show no consistent effects of fencing on Snake River goldenweed populations. Stochastic population growth rates and extinction probabilities appeared to differ at random among the plots. It is apparent that some of the populations (e.g. Lower Lookout, where three out of four study plots had >90% chance of extinction) have an extremely high probability of dropping to low population levels within 50 years. At such small population sizes, the plants are at increased risk of suffering from the deleterious effects of inbreeding and demographic stochasticity (Soulé, 1987).

Compared to other perennial plant species, the observed λ values for Snake River goldenweed are unusually low, especially those observed in the 1991-92, 1994-95, and 1998-01 periods. Most perennials have growth rates near 1.0 unless they are ruderal species such as *Dipsacus* (Caswell 1989), *Hypochaeris* (Kroon et al. 1987), and *Ranunculus* spp. (Sarukhan and Gadgil 1974) in which case they are likely to have very high growth rates (Table 3). The variation in growth rates displayed by *Haplopappus radiatus* appears related to cattle grazing and climatic conditions, which seem to have a large influence on this plant's population dynamics.

Table 3. Equilibrium population growth rates (λ) for several perennial plant species (herbaceous, unless otherwise noted). Populations with λ greater than 1.0 are projected to grow, and those with λ less than 1.0 will decline. The growth rate of a human population is included for comparison.

species	λ	source
Arisaema triphyllum	0.85-1.32	Bierzychudek, 1982
Astragalus australis v. *olympicus*	0.831-1.021	Kaye, 1989
Astrocaryum mexicanum (tree)	0.993-1.040	Pinero et al., 1984
Araucaria cunninghamii (tree)	1.020	Enright and Ogden, 1979
Avicennia marina (mangrove)	1.227	Burns & Ogden, 1985
Calochortus albus	1.336-1.714	Fiedler, 1987
Calochortus obispoensis	0.960-1.031	Fiedler, 1987
Calochortus pulchellus	0.997-1.073	Fiedler, 1987
Calochortus tiburonensis	0.992-1.302	Fiedler, 1987
Chamaelirium luteum	0.990-1.056	Meagher, 1982
Cleistes divaricata	0.982[1]-1.180[2]	Gregg, 1991
Dipsicus sylvestris	2.332	Caswell, 1989
Hypochaeris radicata	1.270-1.946	Kroon et al., 1987
Lesquerella carinata v. *languida*	0.204-2.268	Greenlee, 1994
Lomatium bradshawii	0.919-1.226	Kaye et al., 1993 unpub. data
Mirabilis macfarlanei	0.949	Kaye, 1992
Nothofagus fusca (tree)	0.996-1.028	Enright and Ogden, 1979
Pedicularis furbishae	0.68-1.81	Menges, 1990
Pentaclethra macroloba (tree)	1.002	Hartshorn, 1972 & 1975
Ranunculus acris	0.350-2.328	Sarukhan and Gadgil, 1974
Ranunculus bulbosus	0.093-8.170	Sarukhan and Gadgil, 1974
Ranunculus repens	0.743-1.801	Sarukhan and Gadgil, 1974
Sequoia sempervirens (tree)	0.832-1.235	Namkoong & Roberds, 1974
Stryphnodendron excelsum (tree)	1.047	Hartshorn, 1972 & 1975
Homo sapiens in U.S.A., 1966	1.05	Keyfitz & Flieger, 1971.

[1]calculated from matrix, [2]determined from observed trends

Plant-insect interactions: grasshoppers and seed predators

Herbivory by grasshoppers on Snake River goldenweed appeared to negatively affect seed production in the species. Grasshoppers varied in their impacts, with annual estimates of damage to the plants ranging from an average 11.5% to 64% defoliation over the course of this study (Figure 17). The amount of plant tissue eaten by grasshoppers was negatively

correlated with precipitation during October-December, with the lowest amounts of damage observed after wet falls (Figure 18). Grasshopper population dynamics are relatively complex, and may be affected by seasonal rainfall, temperature, and site productivity, among other factors (Cuningham and Sampson 2000). In a study of grasshopper population dynamics in Colorado, Skinner and Child (2000) found that high October precipitation had a negative effect on grasshopper abundance, possibly due to an increase in pathogens during the cool moist weather. Their results agree with the pattern observed here with data from Snake River goldenweed. Skinner and Child (2000) also found that cool fall temperatures had a negative effect on grasshopper abundances, but this remains to be tested with our current data set.

Seed losses due to insect predators (larvae of weevils, gelechiid moths, and cecidomyiid midges) were generally more significant than losses through natural fruit abortion in 1992, 1994, 1996, 1997, 1998, 2000, and 2001, the reverse of the 1991, 1995, and 1999 situations (no data from 1993 were available), and ranged from 15% to 67% in any given year. Past observations of Snake River goldenweed (Kaye et al. 1990) indicate that seed predation due to insects can be significant, widespread, and due to a large diversity of insects. The population growth and geographical distribution of another *Haplopappus* species, *H. vestitus*, is strongly controlled by insect seed predators that consume a majority of its seeds over a portion of its range (Louda 1982 and 1983). Therefore, the substantial and chronic losses of seeds attributable to insect larvae in Snake River goldenweed may have significant impacts on the long-term population dynamics of this species.

Of the three insect seed predators most often encountered in this study, weevil larvae caused the greatest damage to seeds, damaging an average of nearly 60% of the seeds in flower heads when they were present. Moth and midge larvae damaged fewer seeds, on average (45% and 33% respectively), than weevils. The overall levels of damage varied substantially from year to year, and seed predation was negatively correlated with winter precipitation. The reasons for this correlation are not clear, but may be related to abundance of pathogens affecting these insects during or after wet winters.

Conclusions

This eleven-year study of Snake River goldenweed has documented significant recovery in plant size and reproduction following fencing of populations to exclude livestock. However, there was a substantial delay in this recovery. Depending on the attribute of the plants and their populations, improvement took five to seven years after fencing before it was detected. The frequency of grazing on Snake River goldenweed was also negatively correlated with plant flowering and population growth rate. However, after ten years no negative effects of grazing on population viability were detected.

Seasonal precipitation had significant positive effects on Snake River golden weed flowering, seed production, and population growth, but negative effects on seed predation and grasshopper damage. Seed predation by insects was intense in some years, killing at least half of the seeds in four of the ten years sampled. Grasshoppers also had substantial impacts, consuming over 60% of plant foliage in two of eleven years sampled and negatively affecting seed set. These levels of seed damage and herbivory may have long-term impacts on this species.

Because grazing by livestock had measurable negative impacts on Snake River goldenweed, conservation of the species should consider reducing these effects. Clearly, however, numerous factors affect this species and its long-term survival, including precipitation, grasshoppers, grazing, and other variables not measured here, such as invasive and noxious weeds. It is likely that other populations of this species that occur in similar habitats subject to grazing have smaller plants that reproduce less and have lower population growth rates, on average, than populations in non-grazed areas. Efforts to improve conditions for this species should be given long periods of time to be effective. The exclosures established for this study should be left in place for detection of longer-term effects of fencing on this species. To acquire additional long-term information, the study plots should be resampled at 3-5 year intervals.

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